PER caer; 16064, 16147 PHO cinn; 16155 PER caer; 16160 PHO cinn; 16168 PER schi; 16169 PER vera; 16235 PER schi; 16236 PER caer; 16238 AIO cost; 16239, 16240 PER amer; 16344 OCO insu; 16419, 16421 AIO cost; 16443 PER caer; 16462 PHO cinn; 16469 OCO vala; 16470 PER schi; 16476 OCO pitt; 16556 PHO cinn; 16582, 16587 PER caer; 16588 AIO cost; 16598, 16612 NEC cufo; 18916 PER caer; 20146 PER schi; 20147 PER amer; 24110 OCO vala; 24144 PER vest; 24275 OCO insu; 24307 LIC mult; 24487 OCO vera; 24488 NEC glob; 24540 OCO vera; 24584 OCO nica; 24593 NEC glob; 26512 OCO vera: 26527 OCO flor: 26600 NEC glob: 26612 NEC sali; 28570 PHO cinn; 28623 OCO vala: 28706 OCO oblo: 28732 OCO aura: 28910 PER schi; 28911 PER amer; 28996 OCO vala; 29044 OCO gome.

Williams, R. S.: 319 NEC glob.

Woodson, R. E., et al.: 1022 OCO glau; 1099 PHO

Woodworth, R. H., & P. A. Vestal: 471 OCO cern.

Zamora, N., et al.: 367 NEC niti; 394 NEC reti; 399 LIC sp. A; 410 OCO tene; 442 OCO atir; 674 OCO valo; 719 OCO cern; 729 PHO cinn; 735 PER schi?; 770 NEC memb; 824 NEC sali; 879 OCO hold; 880 OCO pitt; 915 OCO vera; 1014 WIL glau; 1157 NEC sali; 1177 NEC glob; 1208 CAR burg; 1215 BEI oval; 1287 OCO heli; 1300 OCO leuc.

HERNANDIACEAE

By William Burger

REFERENCE—K. Kubitzki, Monographie der Hernandiaceen. Bot. Jahrb. Syst. 69: 78–209. 1969.

Small to medium-sized **trees**, less often shrubs or lianas, usually monoecious (bisexual), rarely dioecious, evergreen or deciduous, nodes unilacunar, oil cells often

present; stipules absent. Leaves alternate in a spiral, simple (in Central America) or palmately compound with 3-5 leaflets, petiolate, leaf blades entire or 3-5-lobed, venation palmate or pinnate. Inflorescences axillary to distal leaves or rarely terminal, dichasial or thyrselike, often with a well-developed primary peduncle and much branched distally, with or without bracts and bracteoles. Flowers usually very small, unisexual or bisexual, radially symmetrical; tepals (sepals) 4-10 in 1 or 2 whorls, free or united at the base; stamens 3-6 in 1 whorl (often opposite the outer whorl of tepals, filaments free, often with 2 basal and lateral or abaxial "glands" (usually narrowed at the base and often cordate), anthers 2-thecous, opening by large flaps from the bottom upward (often remaining attached near the apex of the anther), staminodes absent or glandlike (relationship to glands and interpretation problematical), pollen inaperturate; pistil 1 (carpel apparently 1), ovary inferior and 1-locular, ovule solitary and pendulous from near the apex of the locule, style slender with capitate or broad stigma. Fruits 1-seeded nuts or drupes, with distal wings (in Gyrocarpus), lateral wings (in Illigera), or without wings (enclosed in a cupule of similar texture as the fruits in Hernandia); embryo large, straight, the cotyledons folded or rolled up.

A family of four genera and about 65 species. They are pantropical but with some very unusual, apparently relict, distributions. Many species occur on oceanic island-groups, but the species are not adapted to seaside or littoral vegetation (see Kubitzki, 1969). Costa Rican species are recognized by their unusual fruits (very different in the three different genera), variable and often long petioles, palmately veined leaves (in most) that often vary greatly in size, small or very small flowers with anthers opening by two flaps, and narrow inferior ovary with single locule and ovule. The family appears to be closely related to the Lauraceae with which it shares features of androecial morphology; it differs in the inferior ovary. These plants also resemble some Menispermaceae, both morphologically and in the rarity with which they are collected. While Kubitzki's monograph is excellent, the paucity of collections may require reassessment of species, if and when additional material becomes available.

Key to Species of Hernandiaceae

- 1b. Leaves evergreen or shortly deciduous; without lobes; trees, shrubs and lianas of evergreen forest formations below 1500 m elevation; fruits without wings; flowers unisexual or bisexual 2a

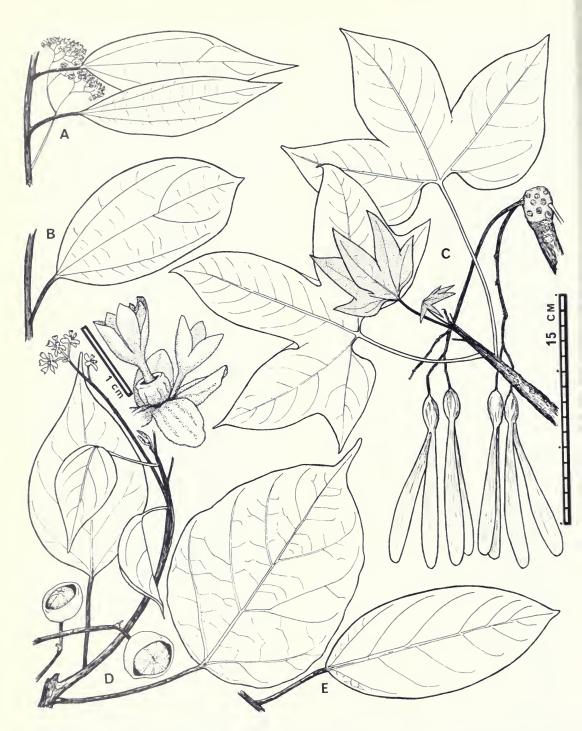


Fig. 23. Hernandiaceae: A, Sparattanthelium amazonum; B, S. septentrionale; C, Gyrocarpus jatrophifolius; D, Hernandia stenura with distal flower-pair; E, H. didymantha.

Gyrocarpus Jacquin

Trees, rarely shrubs, deciduous, bisexual, branches often thick, puberulent or glabrous. Leaves simple, usually clustered at the ends of branches, long-petiolate, leaf blades often broader than long, entire and lobed or unlobed, venation usually palmate, glabrous or puberulent. Inflorescences developing before the leaves or with the leaves present, clustered at the ends of branchlets, flowers usually in small clusters in dichasial, thyrselike or umbellike arrangements, with or without bracts and bracteoles. Flowers bisexual (perfect) or male, very small, parts of the flower often early caducous, perianth usually of 7 (6, 8) parts, 2 parts (lobes) usually much larger and with 2 smaller lobes attached to each large lobe; stamens 4 or 5(-7), filaments free, puberulent or glabrous, anthers opening by 2 valves (flaps) from the bottom upward, 2thecous; staminodes alternating with the stamens or solitary and opposing the style, clavate or thickened and flattened at the apex; ovary inferior and tomentulose, style and stigma 1. Male flowers with reduced ovary, more numerous than perfect flowers, wings not developing. Fruits drupes with 2 long apical oblanceolate wings with rounded tips (narrowly spatulate), developing from primordia within the perianth whorl, basal part (ovary) globose to ovoid or ellipsoid, puberulent to glabrous; seed with leafy cotyledons spirally twisted.

A genus with only three species: one in eastern Africa; G. jatrophifolius from Mexico to central Costa Rica; and G. americanus, with a very unusual pantropical distribution. The genus is distinguished by the unusual 2-winged fruits, inferior ovary, anthers opening by flaps, and restriction to seasonally dry areas. The wings do not develop from the perianth lobes, but rather from a pair of primordia arising interior to the perianth; see discussion in the monograph by Kubitzki (1969).

Gyrocarpus jatrophifolius Domin, Biblioth. Bot. 22, heft 89: 682. 1925 (1926). Figure 23.

Small to medium-sized (5–22 m) trees, occasionally a shrub, bark corrugated with corky ridges, leafy internodes (2–)4–15 mm thick, longitudinally grooved (dry), becoming glabrous and grayish. Leaves usually borne near the ends of stems, petioles 4–28 cm long, 1–5 mm thick, glabrescent and canaliculate above; leaf blades 6–20(–30) cm long, 5–25(–40) cm broad, 3- or 5-lobed, the distal lobes with 2 deep sulci (more than ½ the length of the lobe) and acuminate apices, cordate to truncate at the base with a portion of the major lateral veins forming

part of the lamina base, margins entire, drying thin- to thick-chartaceous, glabrous or minutely (0.1-0.4 mm) puberulent on the veins above and below with thin yellowish hairs, venation palmate with 3 major veins, midvein with 4-8 pairs of major secondary veins. Inflorescences 4-14 cm long and growing longer in fruits, primary peduncles often 1/2 the length of the inflorescence, densely yellowish puberulent, dichasial or thyrselike, often arising from thickened and rounded areas on the stem (these with circular peduncle scars after the infructescences fall off). Flowers small and green, 2-4 mm long; stamens usually 5 (4-7), filaments glabrous or puberulent near the base, 1-3 mm long, anthers ca. 0.6 mm long, dehiscing flaps remaining attached at the apex. Fruits with 2 apical stiffly chartaceous wings, (4.5–)7–11(–13.5) cm long and 7-14 mm broad, broadest above the middle, parallel or spreading and V-shaped, minutely puberulent or glabrescent, base of the fruits (ovary) 16-29 mm long and 6-10 mm thick, ellipsoid to narrowly ovoid, glabrescent or densely tomentulous with yellowish or gray hairs.

Trees of seasonally very dry deciduous forest and woodland formations from near sea level to 900 (1400) m elevation (rarely higher in Guatemala). Flowers have been collected in September—December and March, and fruits have been collected in December—March and May in Central America. The species ranges from Sinaloa, Mexico, southward along the Pacific slope to central Costa Rica.

Gyrocarpus jatrophifolius is recognized by its distinctive fruits with two long narrowly oblanceolate wings above an inferior ovary, the leaves with three prominent distal lobes and two smaller lateral lobes (all with acuminate apices), minute flowers with anthers dehiscing by two flaps, and the restriction to deciduous forest formations. This species is known from only a few collections in Costa Rica made in lowland Guanacaste Province and the western side of the Meseta Central. Kubitzki (1969) distinguished this species from G. americanus Jacq., which has more rounded fruits, leaves that are usually unlobed (in Central America), flowers with usually four stamens, and which reaches its southern limit in northern Nicaragua. Most authors previously have considered the two as parts of a single rather polymorphic species; the two species (as delimited by Kubitzki) are sympatric in northern and central Central America. The name gallito is commonly used for these plants

in El Salvador and Nicaragua; other names are volador, volatin, and caballitos.

Hernandia Linnaeus

Trees, rarely shrubs, monoecious (bisexual), usually evergreen, stems often thick and with soft wood; stipules absent. Leaves simple and alternate, petiolate; leaf blades usually with entire margins (rarely 3-5-lobed), venation pinnate or palmate. Inflorescences usually axillary to distal leaves, corymbiform panicles in Central America, usually with an elongate primary peduncle, inflorescence and bracts usually minutely tomentulous, the distal flower clusters often flower-like because they are subtended by a whorl of 4 sepaloid bracts, the distal flower clusters bisexual with a central female flower (rarely 2 or 3) and 1-4 outer short-pedicellate male flowers, the female flowers subtended by and arising from within a deep cup formed by bracteoles (the cup sessile and with an entire distal margin in our species), bracteoles of the male flowers small and basal or absent. Flowers unisexual, outer perianth parts imbricate, the inner whorl imbricate to valvate, free; male flowers with 6-8 perianth parts (in whorls of 3-6 parts), stamens 3-5(-6), filaments free or united for 1/2 their length, usually each filament with 2 small appendages (glands) near the base; female flowers 4-6-parted, staminodia absent, 4 or 5(-10, 12) free or connate glands present at the base of the style, often opposing the outer perianth segments, ovary inferior and

slightly compressed, style well developed but not exceeding the perianth segments in length, stigma discoidpeltate. Fruits ovoid, ellipsoid, or subglobose drupes, or becoming hard and nutlike, often subtended and enclosed in the expanded and inflated cupule, the cupule often with 8 longitudinal ridges, usually minutely tomentulous (both cups and fruits); cotyledons folded.

A pantropical genus of 24 species best represented in the southwestern Pacific and West Indies with a few species in Africa, Madagascar, Australia, and Central and northernmost South America; see the treatment by Kubitzki (1969). Our species are recognized by the unusual partial inflorescences with two male and one female flower subtended by a whorl of four sepaloid bracts, the female flower arising from within a cup, the anthers opening by two flaps, the inferior ovary and flattened stigma, and the drupelike fruits included within the enlarged cupule. Inflorescence, flowers, and fruits are usually covered by fine minute tomentulose (velutinous) hairs. Soft wood, thick stems, great variation in leaf size and petiole length, and restriction to wet evergreen forests further distinguish our species. These plants are poorly represented in herbaria.

Key to Species of Hernandia

Hernandia didymantha J. D. Smith, Bot. Gaz. 31: 120. 1901. Figure 23.

Trees to over 15 m high, lower branches descending. Leaves simple and unlobed, petioles (1.5-)3-7(-9) cm long, canaliculate above (adaxially); leaf blades 9-18(-21) cm long, 3.5-7 cm broad, oblong to ovate-oblong or slightly obovate, bluntly acute to short-acuminate at apex. obtuse or rounded at the base, margins entire, drying subcoriaceous, glabrous above and below, venation pinnate with (4-)6-8 pairs of major secondary veins, the basal secondaries not more prominent than the distal secondaries. Inflorescences terminal or axillary to distal leaves, paniculate, distal flower clusters usually with only 2 flowers, bracts ca. 8 mm long and 3.5 mm broad, rounded at the apex and becoming reflexed. Male flower usually solitary on a long (5 mm) pedicel, parts in whorls of 3; female flower solitary and very short pedicellate, 4-parted, style with 4 stipitate glands at the base. Fruits 1.8–2.5 cm in diameter, subglobose, conical at the apex, enclosed within a coriaceous cup 2–3 cm in diameter.

This species is only known from lowland evergreen rain forest formations. It has been collected from Punta Mona (Pittier 12682, US, the type), La Selva (Hammel 11656, DUKE; Hartshorn 802, 1026, CR, F; McDowell 606, DUKE), the Golfo Dulce region (Allen 598, F; Q. Jiménez et al. 644, CR, F), and near Almirante, Bocas del Toro, Panama (Cooper 618, Mo). These flowering collections were made in January–April and November. A collection with fruits (Hartshorn 1281, CR, F) from La Virgen de Sarapiquí was made in August. This collection has the fruits almost entirely enclosed by a cupulate receptacle whose distal aperture is

only 3–6 mm wide; see also the photograph in P. E. Sánchez, Florula del Parque Nacional Cahuita, p. 141, 1983, where the fruiting season is said to be September–November.

Hernandia didymantha is recognized by the oblong leaves usually lacking strongly developed basal secondary veins, short acuminate apices, very variable petiole lengths, and characters of the genus. Additional collections may show that this species intergrades with material here treated as H. stenura. If that happens, H. didymantha, the earlier name, would have to be circumscribed more broadly to cover all our material of Hernandia. These trees appear to produce leaves in "flushes" of new growth and it may be that conditions at the time of the leaf flush may determine the size and form of the leaves. If this is the case, it may mean that H. hammelii D'Arcy of Panama is only a small-leaved (6–8 \times 2.5–4 cm) growth form (Ann. Missouri Bot. Gard. 68: 224, 1981). Another recent small-leaved collection is from the Dept. of Yoro, Honduras (Hazlett 2714, F). All this material shows considerable variation in leaf size on the same branch, and all appear to live in the same kinds of moist forests.

Hernandia stenura Standl., Publ. Field Mus. Nat. Hist. Bot. Ser. 18: 1553. 1938. Figure 23.

Trees to over 25 m tall, leafy internodes 1.8-8 mm thick, glabrous or very minutely (0.1 mm) scurfy yellowish puberulent. Leaves simple and unlobed, juvenile and sapling leaves often large and slightly peltate, petioles 5-18 cm long; leaf blades 9-27(-40) cm long, 7-18(-25) cm broad, broadly ovate to ovate-elliptic or ovateoblong, abruptly acuminate at the apex with a tip 1-3.5 cm long (rarely acute), rounded to subcordate at the base, the largest leaves sometimes peltate with the petiole attachment up to 1 cm distant from the lamina margin, drying thick-chartaceous or slightly subcoriaceous, margin entire or somewhat undulate, glabrous above, glabrous or minutely (0.1 mm) grayish puberulent on the veins beneath, venation pinnate or subpalmate with the lowermost secondaries often quite prominent, usually with 3-5 pairs of major secondary veins. Inflorescences 8-30 cm long with prominent primary peduncles 5-20 cm long, paniculate, sweet-scented, the ultimate parts flower-like with usually 4 sepal-like bracts (ca. 10×5 mm) subtending 1 subsessile female flower (and its cupule) and 1-4 pedicellate male flowers, all parts covered with a fine (0.1 mm) dense tomentum of soft hairs white in life but becoming grayish. Male flowers ca. 6 mm long (in bud) on pedicles 4 mm long, parts in whorls of 3, filaments with 2 minute glands; female flowers arising from within cupules ca. 3 mm long, on a short (3–4 mm) pedicel, flower buds ellipsoid, ca. 4-5 mm long, perianth 4-parted. Fruits drupes ca. 2 cm broad and included within the subglobose cupule narrowed at the round distal aperture, fruiting cupule 1.3–2.8 cm long and 1.5–2.8 cm broad (when dry), minutely grayish velutinous/puberulent on all surfaces, distal aperture 1–2 cm broad.

Trees of wet evergreen forest formations from near sea level to 1000 (1400) m altitude; flowers have been collected in November–January and March–May; fruits have been collected in March, June, and September. The species ranges from Guatemala to the province of Coclé in Panama; Costa Rican material has been collected along the Caribbean slope and coastal plain and in the General Valley.

Hernandia stenura is recognized by the long petiolate and broadly ovate leaves with subpalmate venation (sometimes peltate), thick stems with soft wood, distal flower clusters that resemble individual flowers, anthers opening by a flap, and the inferior ovary developing into a drupe that is largely surrounded within a slightly succulent cupule. The cupule is quite distinctive as its distal aperture is entire and somewhat smaller than the enclosed fruits. The dense minute grayish tomentum on all flowering parts is distinctive and reminiscent of that seen in some Lauraceae. These are infrequently collected trees, but they exhibit considerable variation, both between collections and within collections. It is possible that there is intergradation with H. didymantha; see the discussion under that species. Material of this species was mistakenly assigned to H. sonora L. by Standley in "Flora of Guatemala" (Fieldiana, Bot. 24(4): 346. 1946).

Sparattanthelium Martius

Shrubs, small trees, or lianas, evergreen, climbing with recurved hooks (modified short shoots) in some species. Leaves simple and entire, petiolate, leaf blades often narrowly ovate to lanceolate (ovate to obovate), venation palmately tripliveined (rarely pinnate), glabrous or puberulent. Inflorescences axillary from distal leaves, solitary at a node, much branched dichasia with many small distal flowers, bracts and bracteoles absent. Flowers very small, radially symmetrical, apparently bisexual, many are early caducous after anthesis (perhaps functionally male); perianth 4–8-parted, valvate in bud (in 4–5-parted flowers) or imbricate, free to near the base, persisting; stamens 4, 5(-7), alternating with the calyx lobes, filaments glabrous and short, anthers elongate, apiculate at the apex and opening laterally, flaps attached at the apex, both staminodes and glands absent; style straight, stigma discoid or lobed. Fruits developing only on the most distal branches of the infructescence (with very few fruits developing on an infructescence), branches of the infructescence with thickened nodes and somewhat zigzag (fracti-flexuous) in form, both the fruits and the stems

becoming silvery white or yellowish, drupes ovoid to elongate ellipsoid, often with longitudinal ribs; testa chartaceous, embryo, with inrolled cotyledons.

An American genus of 13 species ranging from southern Mexico to Peru, Bolivia, and southern Brazil. The genus is recognized by the usually tripliveined leaves on long slender petioles, the numerous very small flowers on complex inflorescences with apparently dichotomous (but

somewhat unequal) branching, the bisexual flowers with anthers opening by flaps, and the fruits apparently developing only from distal nodose inflorescence branches. Fruits and inflorescence become silvery white in some species. Specimens of this genus have been collected fewer than five times in Central America, but it seems likely that two species occur in southern Central America.

Key to Species of Sparattanthelium

Sparattanthelium amazonum Martius, Flora 24, Beibl 2: 42. 1841, Denkschr. Bayer. Ges. Regensburg 3: 303, t. 11, f. 2. 1841. *S. guatemalense* Standl., Proc. Biol. Soc. Wash. 37: 51. 1924. *S. amazonum* ssp. *guatemalense* (Standl.) Kubitzki, Bot. Jahrb. Syst. 89: 202. 1969. Figure 23.

Shrubs to 6 m tall, scandent or becoming lianas, leafy internodes 0.5-5 cm long, 1.5-4 mm thick, glabrous to densely puberulent with thin grayish straight hairs to 0.6 mm long. Leaves with petioles 1.2-6 cm long, 0.5-1 mm thick, glabrous or puberulent; leaf blades 6-16 cm long, 2.5-5.5 cm broad, lanceolate to narrowly elliptic or elliptic-oblong (rarely ovate), tapering gradually to the acuminate apex, the tip 0.4–1.5 cm long, rounded to obtuse at the base, margin entire or minutely undulate, drying thin-chartaceous, glabrous or puberulent along the major veins above and below, the hairs slender white and straight to 0.7 mm long, venation trinerved from slightly above the base of the lamina (lateral veins form the lamina margin at the very base), midvein with only 1 or 2 pairs of major secondary veins. Inflorescences to ca. 10 cm long, axillary to distal leaves, branches slender and grayish puberulent. Flowers small, ca. 2 mm long, perianth 4 (rarely 5) parted, 1.2–1.5 mm long, 0.4–0.8 mm broad, acute to obtuse at the apex, puberulent; stamens 4 (5), anthers subsessile; ovary (inferior) ca. 0.6 mm long, style slender 1-1.4 mm long. Fruits elongate ellipsoid drupes, ca. 1.7 cm long and 0.8 cm thick, fruits and inflorescences becoming white.

Lianas or shrubs in lowland rain forest formations. Only three collections of this species are known from Central America: *Standley 25066* (type of *S. guatemalensis*) from Puerto Barrios; *Contreras 8957* from Puerto Méndes, both in the Dept. of Izabal, Guatemala; and *Herrera 1210*,

CR, F, MO, from near the Nicaraguan border in Alajuela Province, Costa Rica. Flowers were collected in June and August. Immature fruits were collected by Herrera in November. The other collections of this species are from Brazil and Bolivia.

Sparattanthelium amazonum is recognized by the narrow elliptic acuminate leaves on long slender petioles, the trinerved venation, minute flowers with four perianth parts on thin-branched little inflorescences, and the anthers opening by flaps.

Sparattanthelium septentrionale Sandwith, Kew Bull. 1932: 226. 1932. Figure 23.

Shrubs (perhaps scandent), branchlets conspicuously and densely puberulent in early stages, the hairs slender 0.1-0.5 mm long, leafy internodes 0.8-3 mm thick. Leaves often very variable on the same stem, petioles 1.3–4.2 cm long, slender, puberulent; leaf blades 6-15 cm long, 2-8 cm broad, ovate to elliptic-oblong, abruptly acuminate at the apex with a tip 5-15 mm long, obtuse to rounded at the base, margins entire or slightly undulate, drying chartaceous, puberulent above and below in early stages with slender whitish hairs 0.1-0.8 mm long but the longer hairs falling off, trinerved from the base, the midvein with 2 or 3 pairs of distal secondary veins. Inflorescences said to be 5 cm long (probably becoming larger), branches of the inflorescence slender and gravish puberulent, pedicels to 4 mm long. Flowers about 1 mm in diameter in bud, perianth 5-(6-)lobed, perianth lobes 1.5-2 mm long and 1 mm wide, the lobes elliptic and obtuse at the apex; stamens 5 (4), filaments 0.5 mm long, anthers ca. 1 mm long; style 1.5-2 mm long. Fruits unknown.

Probably confined to lowland evergreen forest formations and known from only three collections,

ranging from Tabasco/Yucatan in Mexico to Costa Rica.

Sparattanthelium septentrionale is distinguished by the broader, more ovate or oblong leaves and the usually 5-parted perianth.

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